MATHEMATICAL MODELS INVOLVING MUTUALISM AMONG SPECIES

A Synopsis

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Mathematical Models Involving Mutualism Among Species

An interaction between two species that benefits both is called mutualism. When the interaction is mandatory for survival of one or both of the species, then it is called obligate. For some time now, a number of articles on mutualistic predator – prey system using ordinary differential equations have appeared in literature e.g. (see [3-5, 11, 17, 23-26]); such models with delay(s) have been considered in [25, 26]. For related work see (2, 6-10, 12-13, 18-19, 22), also.

We will consider both types of models in our study. An important question in such models is to find criteria for co – existence of species for all time. Thus global stability and the persistence for the model are vital criteria. Specifically a system is uniformly persistent if $\exists \delta > 0$ for each component $N(t)$ with $N(0) > 0$, $\lim_{t\to\infty} \inf N(t) \geq \delta$ $(\text{see}[1, 15])$.

The first model we study involves two preys and two predator mutualists:

$$\frac{dx_1}{dt} = x_1 g_1(x_1) - y_1 p_1(x_1, y_2) - y_2 q_1(x_1, y_1)$$

$$\frac{dx_2}{dt} = x_2 g_2(x_2) - y_1 p_2(x_2, y_2) - y_2 q_2(x_2, y_1) \qquad (I)$$

$$\frac{dy_1}{dt} = y_1\{-s_1(y_1) + c_1 p_1(x_1, y_2) + c_1' p_2(x_2, y_2)\}$$

$$\frac{dy_2}{dt} = y_2\{-s_2(y_2) + c_2 q_1(x_1, y_1) + c_2' q_2(x_2, y_1)\},$$

$$x_1(t_0) = x_{10} \geq 0,\ x_2(t_0) = x_{20} \geq 0,\ y_1(t_0) = y_{10} \geq 0 \text{ and } y_2(t_0) = y_{20} \geq 0\,.$$

This is an extension of three species model considered in Freedman et. al. [3]. The variables x_1 and x_2 denote prey densities and y_1 and y_2 are densities of mutualistic predators.

The positive constants c_i and $c_i^{'}, i = 1,2$ denote rate of conversion of prey biomass to predator biomass.

Further we assume the following hypotheses on the given functions,

(H_1)

All functions are continuously differentiable so that solution to i.v.p. (I) exist, are unique and can be continued for all positive time.

(H_2)

$g_i(x_i) : [0,\infty) \to R, g_i(0) > 0, g_i^{'} < 0$; There exist K_i's such that $g_i(K_i) = 0, i = 1,2$. the constants K_1 and K_2 are called carrying capacities of x_1 and x_2 respectively.

(H_3)

The functions $p_i(x_i, y_2),\ i = 1,2$ are predator response functions of the predator y_1. We assume $p_i(0, y_2) = 0, \frac{\partial p_i}{\partial x_i} > 0, i = 1,2$.

These conditions imply that there is no predation in absence of prey and that the predator response function $p_i(x_i, y_2)$ is an increasing function of density x_i.

(H_4)

$\frac{\partial p_i}{\partial y_2} > 0, i = 1,2$. This hypothesis implies that y_2 increases the predation by y_1.

Similarly, we assume

(H_5)

Also $q_i(x_i, y_1)$ satisfy

$q_i(0, y_1) = 0\ ,\ \frac{\partial q_i}{\partial x_i} > 0,\ and \quad \frac{\partial q_i}{\partial y_1} > 0\ ,\ i = 1,2.$

Finally $s_i(y_i)$ denotes the death rate of the predator y_i and $\frac{\partial s_i}{\partial y_i} > 0$, $i = 1,2$.

We will first prove the above model is meaningful, i.e. solutions with positive initial conditions stay positive for all time and that (I) is a dissipative system. We will consider the existence and stability of equilibria. We will also consider the question of existence of periodic solutions, global stability of interior equilibrium and uniform persistence ([3, 9, 24, 25]). We will consider the case of (1) facultative mutualism between predators, (2) facultative – obligate case and the case (3) when mutualism is obligate for both the predators. We will also study the model with time delay (due to gestation for preys). Specifically we will analyze,

$$\frac{dx_1}{dt} = x_1 g_1(x_1) - y_1 p_1(x_1, y_2) - y_2 q_1(x_1, y_1)$$

$$\frac{dx_2}{dt} = x_2 g_2(x_2) - y_1 p_2(x_2, y_2) - y_2 q_2(x_2, y_1) \qquad (II)$$

$$\frac{dy_1}{dt} = y_1\{-s_1(y_1) + c_1 p_1(x_1(t-\tau_1), y_2) + c_1' p_2(x_2(t-\tau_2), y_2)\}$$

$$\frac{dy_2}{dt} = y_2\{-s_2(y_2) + c_2 q_1(x_1(t-\tau_1), y_1) + c_2' q_2(x_2(t-\tau_2), y_1)\},$$

Where $\tau_i \geq 0, i = 1,2$ are delays using gestation. The initial conditions are $x_1(t) = \varphi(t)$, $x_2(t) = \psi(t)$, $t\epsilon[-\eta, 0)$ and $y_i(0) > 0, i = 1,2$. Here $\eta = max\{\tau_1, \tau_2\}$.

The functions φ and ψ are non – negative and continuous.

We also assume that $\varphi(0) > 0$ and $\psi(0) > 0$.

We will study the above model and its submodel in $(x_1 - y_1 - y_2)$, octant for periodic solutions, harmless delays [7, 8, 13], global asymptotic stability [18, 19] and uniform persistence [6, 18].

In the case of non-autonomous system, we will study a four (three) dimensional model (sub model) with periodic coefficients. Specifically we will consider the question, when periodic solutions can occur and their stability (see [14]).

A three – dimensional Kolmogorov model involving one prey and two predators has been studied in [9]. Four dimensional mutualistic models with two predators are considered in [23, 24]. We will also consider a model that involves a mutualist, a prey and n-predators:

$$\frac{du}{dt} = uh(u, x, y_1 \cdots y_n)$$

$$\frac{dx}{dt} = \alpha g(u, x) - \sum_{i=1}^{n} p_i(u, x) y_i \qquad (III)$$

$$\frac{dy_i}{dt} = y_i[-s_i(u, y_i) + c_i(u) p_i(u, x)], 1 \le i \le n,$$

$$u(t_0) = u_0 \ge 0, x(t_0) = x_0 \ge 0, y_i(t_0) = y_{i0} \ge 0, 1 \le i \le n.$$

Here the variable $u(t)$ represents the mutualist's density at time t. The functions $x(t)$ and $y_i(t)$ denote the prey and predator densities at time t. The function h represents the specific growth rate of the mutualist (u) and the function $g(u, x)$ that of prey (x) in the absence of any predation.

The function $p_i(u, x), 1 \le i \le n$, denotes the predator functional response to the prey and mutualist's densities.

The functions $c_i(u), 1 \le i \le n$, are the positive rates of conversion of prey biomass to the predator biomass.

The functions $s_i(u, y_i)$ are the specific death rates of the predator, $y_i, 1 \le i \le n$, in the absence of predation.

Also $\alpha > 0$ is a parameter, we also assume that for $u \ge 0, x \ge 0, y_i \ge 0, 1 \le i \le n$,

(H_1)

$h(0, x, y_1, \cdots y_n) > 0, \frac{\partial h}{\partial u} < 0,$

(H_2)

There exists a unique function $L(x, y_1, \cdots y_n) > 0$ such that $h(L(x, y_1, \cdots y_n), x, y_1, \cdots y_n) = 0.$

The condition (H_1) implies that independent of the $x, y_1, \cdots y_n$ populations u is capable of growing even when rare. Also the growth rate is assumed to be density dependent & decreases as the mutualist population increases.

The condition (H_2) implies that $L(x, y_1, \cdots y_n)$ is the mutualist's carrying capacity and in part specifies in what way the predators and prey become part of the mutualist's environment.

We assume that

(G_1) $\quad g(u, 0) > 0,\ \frac{\partial g(u,x)}{\partial x} < 0\ ,$

(G_2) There exists a unique $K(u)$ such that $g\big(u, K(u)\big) = 0.$

The condition (G_1) implies that the prey population is capable of surviving in the presence or absence of the mutualist and the growth rate in absence of predation is density dependent.

The condition (G_2) implies that $K(u)$ is the carrying capacity of the prey in the absence of predation.

Further, we assume:

(P_1) $\qquad p_i(u, 0) = 0,\ \frac{\partial p_i(u,x)}{\partial x} > 0,\ 1 \le i \le n.$

The above conditions imply that in absence of prey there is no predation. Also, the predator functional response is assumed to be an increasing function of the prey population.

We also assume the death rate is an increasing function of the population $\frac{\partial s_i(u,y_i)}{\partial y_i} > 0$, $1 \leq i \leq n$.

Specifically we will consider the cases when

(I) There is facultative mutualism between u & x,

(II) There is facultative mutualism between u & y_i (for a fixed $i, 1 \leq i \leq n$),

(III) There is obligate mutualism between u & y_i (for a fixed $i, 1 \leq i \leq n$),

We will subject the above model to the following analysis:

Show that system is dissipative. Study existence of equilibria, their local and global stability, existence of periodic solutions and persistence (see[17, 23, 24]).

In the case of obligate mutualism between u & y_i the conditions of reversal of outcome will be obtained, i.e. when mutualist's presence implies uniform persistence in the system that otherwise exhibits extinction.

We will also consider the time delay (due to gestation) version of model (II) (see [6, 7, 8, 18, 19])).

Finally we will consider the harmless delays for a general linear time delay system as in [13, 16, 20, 21].

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